

Abstract—Sex-specific demography and reproductive biology of stripey bass (*Lutjanus carponotatus*) (also known as Spanish flag snapper, FAO) were examined at the Palm and Lizard island groups, Great Barrier Reef (GBR). Total mortality rates were similar between the sexes. Males had larger L_{∞} at both island groups and Lizard Island group fish had larger overall L_{∞} . Female:male sex ratios were 1.3 and 1.1 at the Palm and Lizard island groups, respectively. The former is statistically different from 1, but is unlikely significantly different in a biological sense. Females matured on average at 2 years of age and 190 mm fork length at both locations. Female gonadal lipid body indices peaked from August through October, preceding peak gonadosomatic indices in October, November, and December that were twice as great as in any other month. However, ovarian staging revealed 50% or more ovaries were ripe from September through February, suggesting a more protracted spawning season and highlighting the different interpretations that can arise between gonad weight and gonad staging methods. Gonadosomatic index increases slightly with body size and larger fish have a longer average spawning season, which suggests that larger fish produce greater relative reproductive output. Lizard Island group females had ovaries nearly twice as large as Palm Island group females at a given body size. However, it is unclear whether this reflects spatial differences akin to those observed in growth or effects of sampling Lizard Island group fish closer to their date of spawning. These results support an existing 250 mm minimum size limit for *L. carponotatus* on the GBR, as well as the timing of a proposed October through December spawning closure for the fishery. The results also caution against assessing reef-fish stocks without reference to sex-, size-, and location-specific biological traits.

Manuscript approved for publication 22 July 2003 by Scientific Editor.
 Manuscript received 22 July 2003 at NMFS Scientific Publications Office.
 Fish Bull. 102:94–107 (2004).

Sex-specific growth and mortality, spawning season, and female maturation of the stripey bass (*Lutjanus carponotatus*) on the Great Barrier Reef

Jacob P. Kritzer

School of Marine Biology & Aquaculture
 and CRC Reef Research Centre—Effects of Line Fishing Project
 James Cook University

Townsville, Queensland 4811, Australia

Present address: Department of Biological Sciences
 University of Windsor
 401 Sunset Avenue
 Windsor, Ontario N9B 3P4, Canada

E-mail address: kritzer@uwindsor.ca

Lutjanid snappers are among the most prominent species comprising the catch of hook-and-line fisheries on tropical reefs worldwide (Dalzell, 1996). A notable exception is the line fishery on Australia's Great Barrier Reef (GBR). There, the finfish catch, and therefore the majority of fisheries research, is dominated by coral trouts of the genus *Plectropomus* (Mapstone et al.¹). However, the GBR finfish harvest is diverse and the catch of many secondary species has risen steadily since the early 1990s (Mapstone et al.¹). Furthermore, over the past decade, the GBR fishery has changed with the advent of the lucrative Asian live reef-fish market. At present, only a handful of the many species harvested on the GBR are exported to the live reef-fish market. However, continued expansion of the trade coupled with the depletion of fish stocks in other source nations (Bentley²) has the potential to introduce demand for a wider range of species. Even in the absence of changes in the species composition of live reef-fish exports, increased demand for secondary species due to changes in either domestic preferences or availability of primary species has the potential to elevate harvest of currently nontarget species (Kritzer, 2003).

Effective multispecies management of the GBR fishery will ultimately require understanding the biology of more than simply the primary target species. For example, spawning closures of the fishery have been proposed for nine-day

periods around the new moon in October, November, and December on the rationale that this will protect spawning activity of a wide range of harvested species (Queensland Fisheries Management Authority³). Yet, spawning season information for species beyond the common coral trout (*P. leopardus*) (Ferreira, 1995; Samoilys, 1997) is nearly nonexistent. The GBR fishery is in a fortunate position with respect to management of many species for which exploitation is still at relatively low levels because baseline biological characteristics can be estimated before stock structure is drastically altered by fishing. These data can then be used in both formulating management strategies and monitoring effects of fishing.

¹ Mapstone, B. D., J. P. MacKinlay, and C. R. Davies. 1996. A description of the commercial reef line fishery log book data held by the Queensland Fisheries Management Authority. Report to the Queensland Fisheries Management Authority, 480 p. Primary Industries Building, GPO Box 46, Brisbane, Queensland 4001, Australia.

² Bentley, N. 1999. Fishing for solutions: can the live trade in wild groupers and wrasses from Southeast Asia be managed? TRAFFIC Southeast Asia report, 143 p. Unit 9-3A, 3rd Floor, Jalan SS23/11, Taman SEA, 47400 Petaling Jaya, Selangor, Malaysia.

³ Queensland Fisheries Management Authority. 1999. Queensland coral reef fin fish fishery. Draft management plan and regulatory impact statement, 80 p. Primary Industries Building, GPO Box 46, Brisbane, Queensland 4001, Australia.

One of the most prominent secondary species in the GBR fishery is the stripey bass (*Lutjanus carponotatus*) (Spanish flag snapper, FAO). In relation to other large predators on the GBR, *L. carponotatus* is highly abundant on inshore reefs, common on mid-continental shelf reefs, and absent from outer-shelf reefs (Newman and Williams, 1996; Newman et al., 1997; Mapstone et al.⁴). Although this affinity for inshore reefs has the potential to make the species more susceptible to recreational fishing, the limited available data do not suggest that it is heavily exploited by the recreational fleet (Higgs, 1993) in relation to the commercial fleet (Mapstone et al.¹). *Lutjanus carponotatus* has a broad-based diet, consuming a wide variety of smaller reef fishes and invertebrates (Connell, 1998). Its role as a predator coupled with its abundance, particularly on inshore reefs, suggests that the species might have an important ecological function on the GBR in addition to its role as a fishery resource.

Davies (1995) and Newman et al. (2000) have collected basic demographic data for *L. carponotatus* on the northern and central GBR, respectively. They both reported a pronounced asymptote in the growth trajectory and that most growth occurred over the first three to five years and little subsequent growth over a lifespan that can reach 15 to 20 years. Newman et al. (2000) also reported a heavily male-biased sample and larger body sizes among males. Unlike age and growth data, no information on reproduction of *L. carponotatus* has been available despite that fact that existing (minimum size limits) and proposed (spawning closures) fisheries regulations are based largely on reproductive traits (Queensland Fisheries Management Authority³).

Specific aims of this study were 1) to estimate sex ratios and sex-specific schedules of growth and mortality; 2) to estimate age- and size-specific schedules of female maturation; 3) to identify the spawning season; and 4) to determine whether reproductive output is proportional to body size by examining the ovary weight-body weight relationship and the average spawning duration of large and small fish. All traits were estimated at the Palm Island group on the central GBR. Additionally, sex-specific growth and female maturity schedules were also examined at the Lizard Island group on the northern GBR to develop spatial comparisons.

Materials and methods

Field methods

Size, age, and reproductive data were obtained for 465 *L. carponotatus* collected by spear fishing on fringing reef slopes during monthly fishery independent sampling at

Pelorus, Orpheus, and Fantome Islands in the Palm Island group on the central GBR (Fig. 1) from April 1997 through March 1998. No sampling took place in January 1998 because of severe flooding in the area. To develop spatial comparisons, samples of 118 and 18 fish were obtained in October 1997 and April 1999, respectively, by spear fishing at the Lizard Island group approximately 400 km north of the Palm Island group (Fig. 1). Fish were collected from depths of 2 to 15 m by teams of two to four scuba divers. *Lutjanus carponotatus* most commonly inhabits depths less than 15 m (Newman and Williams, 1996); therefore sampling efforts encountered the majority of the population. Fish were targeted as encountered, without preference based on size, in order to collect as representative a sample as possible. Fish <150 mm fork length (FL) were rare in the samples because they were infrequently observed on reef slopes (Kritzer, 2002). Therefore, supplemental spear fishing on reef flats targeting smaller fish was conducted at the Palm Island group ($n=24$) in April and December 1999 and at the Lizard Island group ($n=25$) in May 1999 to obtain growth data for size classes against which the primary sampling was biased.

Total weight (TW, g) and FL (mm) of each specimen were recorded. Ovaries and testes of small lutjanids on the GBR are characterized by a lipid body running along the length of each lobe, akin to that found in tropical acanthurids (Fishelson et al., 1985). Gonads and these associated lipid bodies were removed and preserved in FAAC (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%). Sagittal otoliths were removed, cleaned, and stored for later analyses.

Gonad processing and ovarian staging

The lipid body was removed from each ovary or testis after fixation and the weight of the gonad (GW) and lipid body (LW) were measured to the nearest 0.01 g. A gonadosomatic index (GSI) and lipidsomatic index (LSI; after Lobel, 1989) were calculated for each sample as the percentage of TW represented by GW and LW, respectively. Features of whole fixed ovaries including color, speckling, and surface texture were noted as potential criteria for macroscopic staging after comparison with samples processed histologically. Sex of the April 1999 Lizard Island group samples was determined macroscopically only, and was therefore used in sex-specific growth analyses but not in analysis of maturity. Fish <150 mm FL had undeveloped gonads and sex of these specimens was not determined or assigned a reproductive stage.

A subsample of 131 ovaries spanning the range of gonad sizes and external appearances were prepared for histological examination. Samoily and Roelofs (2000) found that medial gonad sections were adequate for determination of reproductive status. Therefore, a medial section was removed from one gonad lobe, dehydrated, and embedded in paraffin. Embedded ovarian tissues were sectioned at 5 μ m and stained with hematoxylin and eosin. Ovaries were staged on the basis of the most advanced oocyte stage present (West, 1990). Additional features used in histological staging included the presence of brown bodies and atretic

⁴ Mapstone, B. D., A. M. Ayling, and J. H. Choat. 1998. Habitat, cross shelf and regional patterns in the distributions and abundances of some coral reef organisms on the northern Great Barrier Reef. Great Barrier Reef Marine Park Authority research publication 48, 71 p. GPO Box 1379, Townsville, Queensland 4810, Australia.

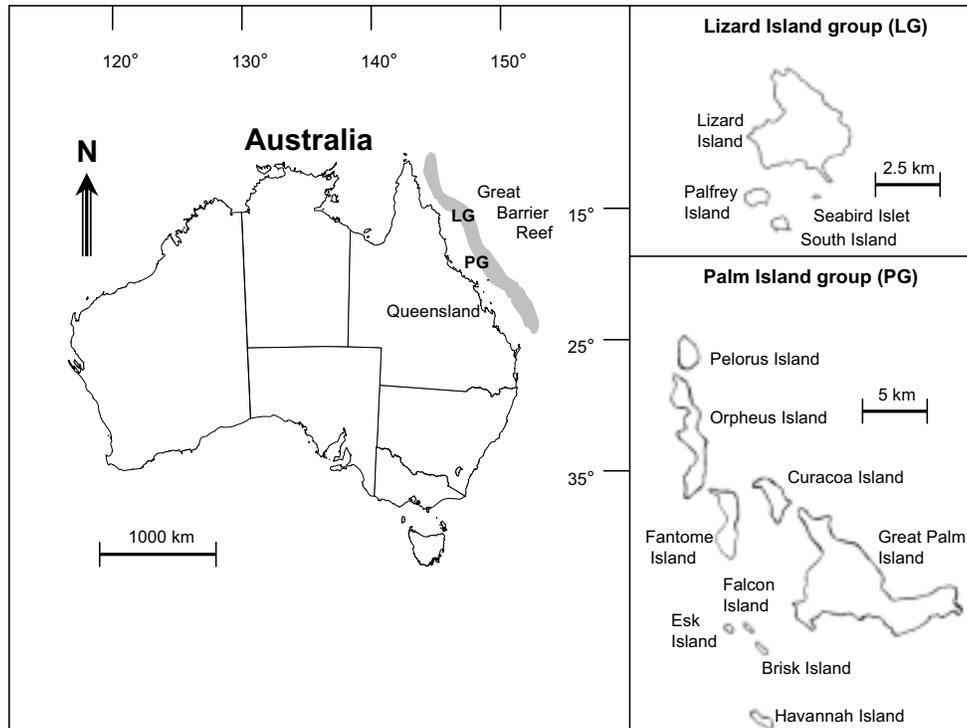


Figure 1

Location of the Palm Island group (PG) and Lizard Island (LG) group within the Great Barrier Reef off the coast of Queensland, Australia.

oocytes and, in the case of inactive ovaries, the relative thickness of the gonad wall and the compactness of the ovarian lamellae (Samoilys and Roelofs, 2000). For those samples processed histologically, macroscopic features were compared within and between reproductive stages to determine whether any macroscopic characteristics could be used to accurately stage ovaries

Age determination

Ages of fish were determined in order to estimate age-based schedules of growth, mortality, and maturation. Otoliths lacking broad, opaque macro-increments were processed to enumerate finer presumed daily micro-increments. These otoliths were ground by hand first from the anterior end and then the posterior end through a progressively finer series of P1200 sandpaper, 12- μ m lapping film, and 9- μ m lapping film until a thin section through the nucleus remained. Micro-increments were enumerated on two independent occasions. If the two counts for one specimen did not deviate by more than 5% of their mean, the mean was used as the age estimate. Otherwise, a third reading was performed and the mean of this and the more similar of the first two readings was used as the age estimate, again provided that the counts differed by no more than 5% of their mean.

Macro-increments in the otoliths of *L. carponotatus* have been validated as annuli by tetracycline labeling (Cappo et al., 2000). A pilot analysis indicated that age estimates did

not differ between readings of whole left and right otoliths (paired *t*-test: $df=59$; $t=0.60$; $P=0.55$); therefore one otolith was randomly selected from each sample for age determination. All otoliths were initially read whole. A second pilot analysis compared whole and sectioned age estimates for a subsample of *L. carponotatus* otoliths. This comparison suggested that whole readings began to drastically underestimate age beyond approximately sectioned age 12 (see Kritzer, 2002). To capitalize on both the greater efficiency of whole readings and the greater accuracy of sectioned readings, whole readings were used for all fish except for those for which any whole reading exceeded 10 or for which there was not agreement in at least two out of three independent whole readings. If at least two out of three independent readings of either whole or sectioned otoliths (as appropriate) agreed, then that value was used as the age estimate. Ferreira and Russ (1994) have described the whole- and sectioned-otolith preparation and reading methods used in the present study.

Sex-specific demography

Early growth of *L. carponotatus* was estimated by linear regression of FL on age for those samples processed to read subannual micro-increments. Separate regressions were performed for the Palm and Lizard island groups and these were compared by analysis of covariance (ANCOVA). Because of the undeveloped nature of the gonads of the smallest fish, early growth was estimated without refer-

ence to sex. Sex ratios at each island group were compared with an expected ratio of 1:1 by χ^2 goodness-of-fit tests by using all specimens (i.e. immature and mature) whose sex could be determined.

Lifetime growth parameters were estimated for males and females from each island group by fitting the von Bertalanffy growth function (VBGF),

$$L_t = L_\infty(1 - \exp(-K(t - t_0))),$$

where L_t = FL at age t ;

L_∞ = the mean asymptotic FL;

K = the Brody growth coefficient; and

t_0 = the age at which fish have theoretical FL of 0.

Growth functions were fitted by nonlinear least-squares regression of FL on age by using samples for which sex was determined. Because VBGF parameter estimates can be sensitive to the range of ages and sizes used (see Ferreira and Russ, 1994, for an empirical example), a common t_0 equivalent to the x -intercept of the early growth estimates was used in all models (see "Results" section). Although the sex-specific sample sizes at the Lizard Island group were smaller ($n=65$ for females; $n=62$ for males), VBGF parameter estimates achieved high precision at sample sizes between 50 and 100 (Kritzer et al., 2001); therefore the Lizard Island group data were included in the analysis. Growth parameters were compared by plotting 95% confidence regions of the parameters K and L_∞ (Kimura, 1980) for each sex from each location and assessing the degree of overlap.

Sex-specific total mortality rates, Z , were estimated by using the age-based catch curve of Ricker (1975) as the slope of a linear regression of natural log-transformed frequency on age class. Everhart and Youngs (1981) proposed that catch curve analysis should exclude age classes with $n < 5$ and Murphy (1997) proposed that age structures used in catch curves should be truncated at the first age class with $n < 5$. Alternatively, Kritzer et al. (2001) proposed that a sample should contain an average of at least ten fish per age class irrespective of age class-specific sample sizes. Therefore catch curves were fitted by two different methods for each sex at the Palm Island group. The first catch curve began at the modal age class and stopped before the first age class with $n < 5$. The second catch curve likewise began at the modal age class but included all age classes that were thereafter represented in the data set. Sex-specific sample sizes for the Lizard Island group were too small by any of these criteria and this location was excluded. Mortality estimates for Palm Island group fish were compared between the fitting methods within each sex as well as between sexes by ANCOVA.

Reproductive biology

Maturation schedules of female fish were estimated for each island group by fitting a logistic model,

$$P_i = 1 / (1 + \exp(a - ri)),$$

where P_i = the proportion of mature fish in age or 20-mm size class i ;

a adjusts the position of the curve along the abscissa; and

r determines its steepness.

Age- and size-specific maturity functions were used to estimate the mean age, t_{50} , and size, L_{50} , at which 50% of females are mature at each island group.

Monthly mean LSI and GSI values of mature Palm Island group fish were plotted separately for males and females to determine seasonal patterns of energy storage and the peak spawning period of *L. carponotatus*. The proportion of specimens at each mature female reproductive stage in each month was also plotted to examine ovarian development patterns throughout the year and the degree of spawning activity occurring outside of peak months.

To examine whether relative reproductive output increases with body size, GW and GSI for stage-IV ovaries collected during peak spawning months were regressed against TW. Residual plots were used to assess deviation from a linear relationship and to identify three outliers, which were removed from the regression analysis. Regression slopes were compared between the two island groups by ANCOVA. Also, mean GSI values and the proportion of Palm Island group females with stage-IV ovaries during spawning months were compared between females ≤ 230 mm FL and those > 230 mm FL to examine whether the duration of spawning varies between size classes (*nota bene*: 230 mm FL is approximately the mean size of mature Palm Island group females and splits each month's sample approximately in half).

Results

Ovarian staging

Five female reproductive stages were identified through histological analysis (Table 1) and were based largely on the scheme of Samoilys and Roelofs (2000). Ovarian stages I (immature) and II (resting mature) have similar oocyte stages. These can be distinguished by the presence of brown bodies or atretic oocytes, which are typically products of prior spawning (e.g. Ha and Kinzie, 1996; Adams et al., 2000) and are usually absent from stage-I ovaries. However, these structures will not necessarily persist in ovaries that have spawned, and in fact were rare among the samples; therefore identification of immature females was based primarily on structural organization of the ovary. Stage-I ovaries typically have a thin ovarian wall and more compacted oocytes, whereas ovaries that have previously spawned tend to have a thicker ovarian wall and a more disorganized arrangement of oocytes (Table 1). Also, there were distinct size differences between stage-I ovaries and other stages. The mean GW of stage-I ovaries was approximately one-third that of stage-II ovaries, and mean GSI was approximately one-half of that at stage II (Table 1), and the distribution of body sizes of fish at stage I had much lower minimum, maximum, and modal size

Table 1

Description of histological and macroscopic features (after fixation in a formaldehyde, acetic acid, calcium chloride solution) of ovarian developmental stages of *Lutjanus carponotatus*. Stage definitions and descriptions are largely a modification of the scheme proposed by Samoily and Roelofs (2000). Mean ovary weight (GW) and gonosomatic index (GSI) for the larger Palm Island group sample are provided.

	Stage	Histological features	Macroscopic features
Inactive	I Immature	Relatively thin ovarian wall; lamellae well packed; only darkly purple staining previtellogenic oocyte stages (oogonia and perinucleolar stages) present.	Always even white color over entire surface; smooth surface texture; lobes quite small (typically <2 cm long) and thin (mean GW=0.33 g; mean GSI=0.24%).
	II Resting	Relatively thick ovarian wall; spaces between lamellae common; only previtellogenic oocyte stages and possibly brown bodies and few atretic vitellogenic oocytes present.	Even white to cream or tan color over gonad surface; surface may be smooth or somewhat convoluted; small white stage II ovaries are difficult to distinguish from stage I without histology (mean GW=1.01 g; mean GSI=0.43%).
Active	III Ripening	Most advanced oocytes are at yolk globule or migratory nucleus stage; atretic oocytes or brown bodies possibly present.	Color sometimes white but more often cream to tan; surface is commonly convoluted; difficult to distinguish from stage II without histology (mean GW=1.18 g; mean GSI=0.53%).
	IVa Ripe	Most advanced oocytes at yolk vesicle stage; atretic oocytes or brown bodies possibly present.	Color tan to brown or mustard with opaque speckles that become larger and more dense as late stage oocytes become more numerous; convoluted surface sometimes with prominent vascularization (mean GW=4.04 g; mean GSI=1.39%).
	IVb Running ripe	Similar to stage IVa but large, irregularly shaped, clear to lightly coloured hydrated oocytes are present.	External appearance identical to stage IVa and can only be differentiated histologically (no samples found at Palm Island group).

classes compared with the distribution of body sizes of fish at stage II (Fig. 2).

Stage-III (ripening) ovaries contain oocytes at the yolk vesicle vesicle stage, which some authors classify as vitellogenic (e.g. Samoily and Roelofs, 2000) and others classify as previtellogenic (e.g. West 1990). Like stage-II ovaries, stage-III ovaries can, but do not necessarily, contain brown bodies or atretic oocytes as evidence of probable prior spawning. Although the fish might not have spawned previously, stage III is considered to be a mature stage in the present study because the appearance of yolk vesicles is associated with the initial development of the yolk globule and represents advanced development of the oocyte beyond perinucleolar stages (West, 1990). Therefore, the fish is preparing for spawning and will soon be part of the mature population if it is not already. Mean age and size of stage-II (4.4. years and 219 mm FL), stage-III (5.0 years and 222 mm FL), and stage-IV (6.5 years and 261 mm FL) females were much more similar to one another than they were to stage-I females (1.9 years and 119 mm FL). Moreover, size-frequency distributions of fish at stages II, III, and IV showed considerable overlap and similarity with one another and were all quite distinct from the size-frequency distribution for stage-I females (Fig. 2). This suggests a division between immature fish and those that are spawning or are nearly ready to do so. The pronounced difference

in GW and GSI between stage-I and stage-III ovaries and similarity in these metrics between stage-II and stage-III fish (Table 1) further support this division.

Most immature ovaries and all ripe ovaries could be identified macroscopically. Because certain macroscopic features were common to multiple ovarian stages, additional histological features was required to separate the largest immature from the smallest resting ovaries and all ripening from resting ovaries among the samples remaining after the initial comparison between histological and macroscopic features. Only one ovary with fully hydrated oocytes, collected at the Lizard Island group, was found among the samples prepared for histological analysis; therefore stages IVa and IVb were treated as a single stage. Stage IV sufficiently represents final development toward spawning on the broad seasonal time scale adopted in this study but encompasses a wide range of ovarian characteristics and would need to be divided into more detailed stages for finer temporal scale studies of lunar or diel spawning patterns. No samples exhibited features of truly "spent" ovaries.

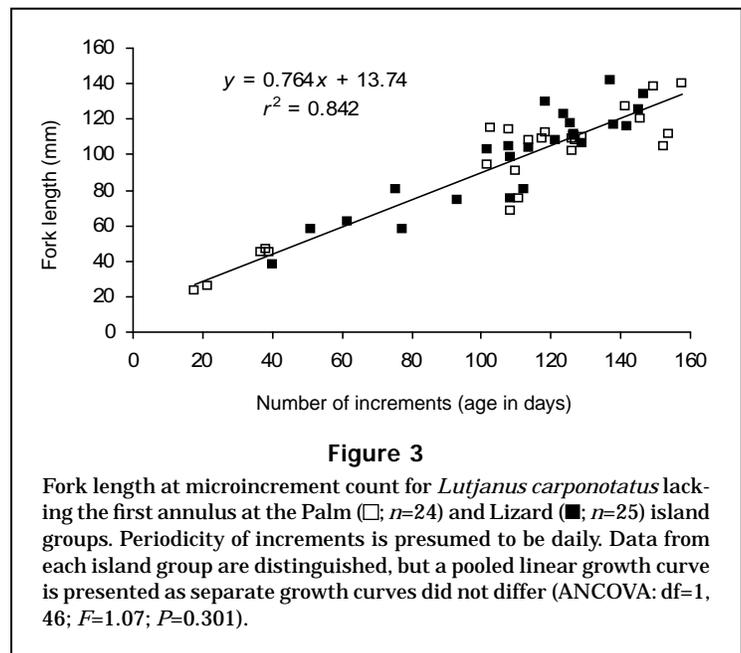
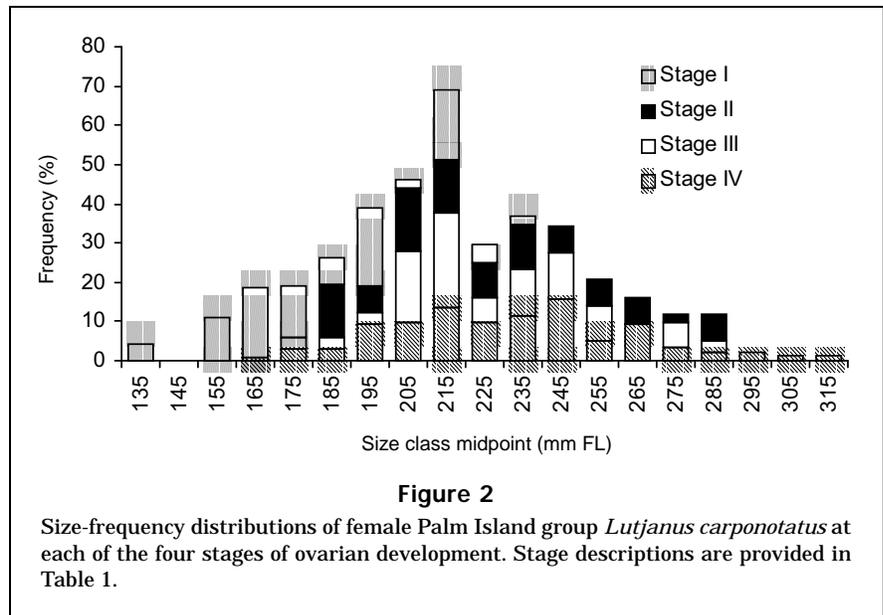
Sex-specific demography

Differences were not apparent in early growth of *L. carponotatus* between the island groups (ANCOVA: $df=1, 46$; $F=1.07$; $P=0.301$); therefore the data were pooled to

estimate an early growth rate of 0.76 mm/d, assuming daily periodicity of micro-increments (Fig. 3). This rate of growth represents quite rapid growth, given that fish are adding 100 mm of length in around 4 months, increasing from approximately 20 to 120 mm FL (Fig. 3). The x -intercept of the early growth curve ($=-17.98$ d) was divided by 365 d/yr to estimate a common t_0 ($=-0.049$ yr) for all VBGF models.

Although size at age for both sexes at both island groups was characterized by substantial individual variability, different growth trajectories were evident for males and females (Fig. 4, A and B). Estimates (Table 2) and 95% joint confidence regions (Fig. 4C) for the VBGF parameters indicated that the primary differences in these trajectories at each island group lay in L_∞ (which indicated that males grow larger than females). In contrast, the common range of K values spanned by the sexes within each island group indicated similar curvature (Table 2, Fig. 4C). However, use of a common t_0 restricts the range of possible fitted K values (Kritzer et al., 2001). In addition to the differences between the sexes, the data revealed a general pattern of larger body sizes at the Lizard Island group (Table 2, Fig. 4).

Mortality estimates at the Palm Island group were slightly higher when all age classes beyond 1 year were included compared with exclusion of age classes with $n < 5$ (Fig. 5). These higher mortality estimates contrast with Murphy's (1997) finding that truncation of the age structure results in higher least-squares estimates of Z . The differences between mortality rates estimated with and without age classes with $n < 5$ were minor for both males (ANCOVA: $df=1, 20; F=0.009; P=0.92$) and females (ANCOVA: $df=1, 23; F=1.35; P=0.26$). Therefore, for comparisons between the sexes, the estimates that included all age classes greater than 1 yr were used. In contrast to the sex-specific growth differences, Z estimates of 0.26/yr and 0.29/yr (Fig. 5) corresponding to annual survivorship of 77% and 75% for females and males, respectively, at the Palm Island group were similar between the sexes (ANCOVA: $df=1, 27; F=0.505; P=0.483$). Murphy's (1997) results also suggested that least-squares mortality estimates are likely to be around 30% less than the true mortality rate when $n = 200$ and the true $Z = 0.2$ /yr. Correcting these mortality estimates based upon this potential bias results in Z estimates up to 0.37/yr and 0.41/yr for females and males, respectively, with corresponding annual survivorship of 69% and 66%. However, the catch curve estimates (Fig. 5) corresponded well with estimates based upon Hoenig's (1983) empirically derived relationship between Z and



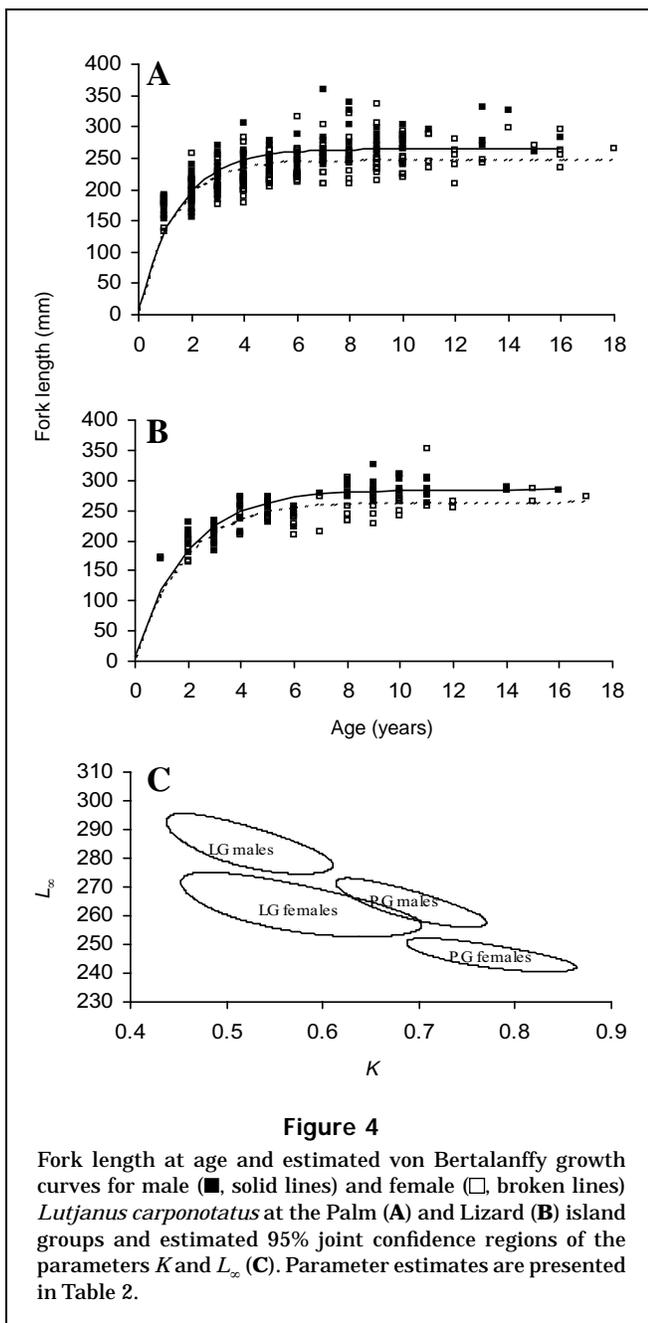
maximum age, t_{max} (females: $t_{max}=18$ yr, $Z=0.23$ /yr; males: $t_{max}=16$ yr; $Z=0.26$ /yr).

The observed female-to-male sex ratios of 1.3 and 1.1 were close to unity at the Palm and Lizard Island groups, respectively (Table 2). However, χ^2 tests suggest this ratio is statistically different from 1 at the Palm Island group ($df=1; \chi^2=7.74; P=0.005$) but not at the Lizard Island group ($df=1; \chi^2=0.031; P=0.86$).

Age and size at maturity

Although there was some indication that Palm Island group females mature at slightly younger ages and smaller sizes

than Lizard Island group females, maturation schedules were generally similar (Fig. 6). At both island groups, age 2 was the age at both earliest maturity and 50% maturity, and 93–100% of females had matured by age 4 (Fig. 6A, Table 3). Thus, maturation was rapid, beginning early in life and ending within a 2-year period with nearly all members of a cohort mature. Length-specific maturation schedules also exhibited similarity between the island groups with mature fish first appearing in the 160–179 mm FL size class, estimated 50% maturation in the 180–199 mm FL size class, and 93–100% maturity at the 220–239 mm FL size class (Fig. 6B, Table 3).



Spawning season

Mature female LSI values were highest in August through October with a maximum in September (Fig. 7A). The peak in GSI lagged that of LSI by two months with the highest values occurring from October through December and with a maximum in November (Fig. 7A). The absence of a January sample unfortunately leaves some ambiguity as to whether GSI, and therefore presumably spawning activity, would still be high at this time or if it would have begun to decline. Male GSI values also exhibited a November maximum (Fig. 7B). Male LSI values, however, did not show any clear trend of increase and decline throughout the year and peaks in April, May, and August that did not correlate with future GSI values as clearly as seen in the female data (Fig. 7). Unlike LSI values for females, monthly mean male LSI values were always greater than the corresponding GSI values.

The seasonal pattern of *L. carponotatus* spawning activity suggested by monthly trends in the proportions of mature ovarian stages can be interpreted as different from that suggested by GSI values. The lowest GSI values in the October–December peak period were close to twice as great as the next highest values in September and February (Fig. 7A). However, the percentage of stage-IV ovaries in the September sample was greater than 50%, which is well over half the percentage of the October sample; whereas the February sample comprised approximately the same percentage of stage-IV ovaries as October (Fig. 8). Also, more than 50% of the March sample was stage-IV ovaries (Fig. 8), whereas its GSI value was close to that of the months with relatively few ripe ovaries (Fig. 7A). Furthermore, September and March had the highest proportions of ripening (stage-III) females and thus far fewer resting mature (stage-II) females than the April to August period of limited spawning activity (Fig. 8). Therefore, regardless of whether September, February, and March are defined as nonspawning months or months of limited spawning activity based upon GSI, analysis of ovarian stage frequencies suggests these to be periods of greater spawning activity than might be predicted with GSI. Clearly, the presence of advanced oocytes is a much better indication of imminent spawning than any measure of gonad size; therefore the reproductive stage-frequency data undoubtedly provide the more accurate picture of *L. carponotatus* spawning patterns.

Of 59 ovaries staged from the October 1997 Lizard Island group sample, eight were at stage I, two were at stage II, and 49 (96% of mature females in the sample) were at stage IV. This finding suggests that the island groups share at least October as a common period of active spawning.

Reproductive differences between locations and among size classes

The variation in GW among females of like body sizes during peak spawning months increased to some degree with increasing TW, but there was a generally homogeneous spread of data around the predicted regression

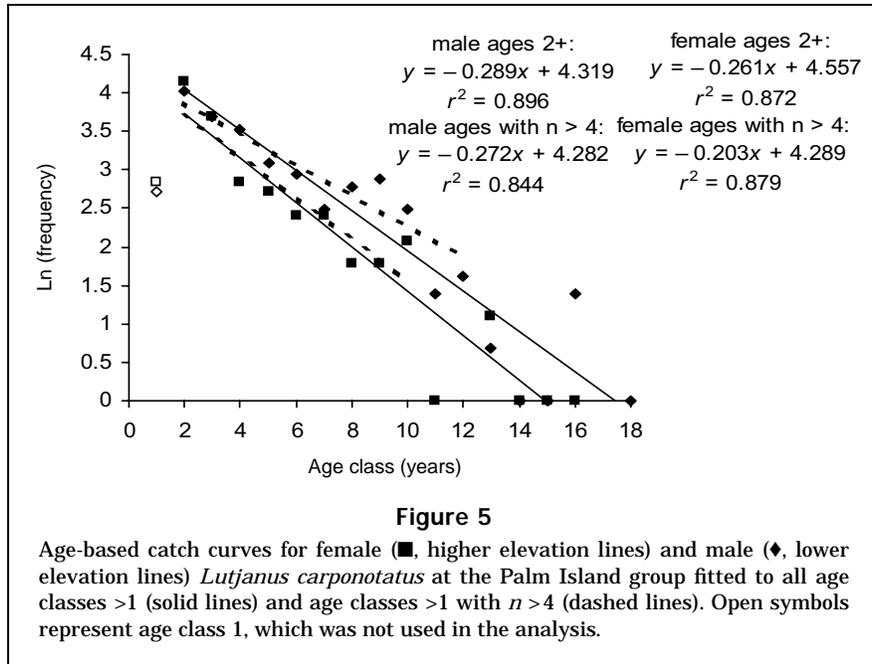


Table 2

Sex-specific von Bertalanffy growth parameters for *Lutjanus carponotatus* at the Palm and Lizard Island groups, Great Barrier Reef. n is sample size; \bar{L}_F is the mean fork length (mm); K is the Brody growth coefficient (per yr); L_∞ is the mean asymptotic fork length (mm); a common t_0 of -0.049 yr was used in all growth models. Standard errors are provided below parameter estimates.

	n	\bar{L}_F	K	L_∞	r^2
Palm Island group					
females	263	224.2 (2.11)	0.77 (0.032)	246.3 (2.25)	0.515
males	202	224.7 (2.78)	0.69 (0.028)	264.3 (3.26)	0.629
sex ratio	1.3:1				
Lizard Island group					
females	65	239.9 (4.76)	0.56 (0.043)	263.5 (4.24)	0.618
males	62	256.4 (4.77)	0.51 (0.032)	284.8 (4.03)	0.714
sex ratio	1.1:1				

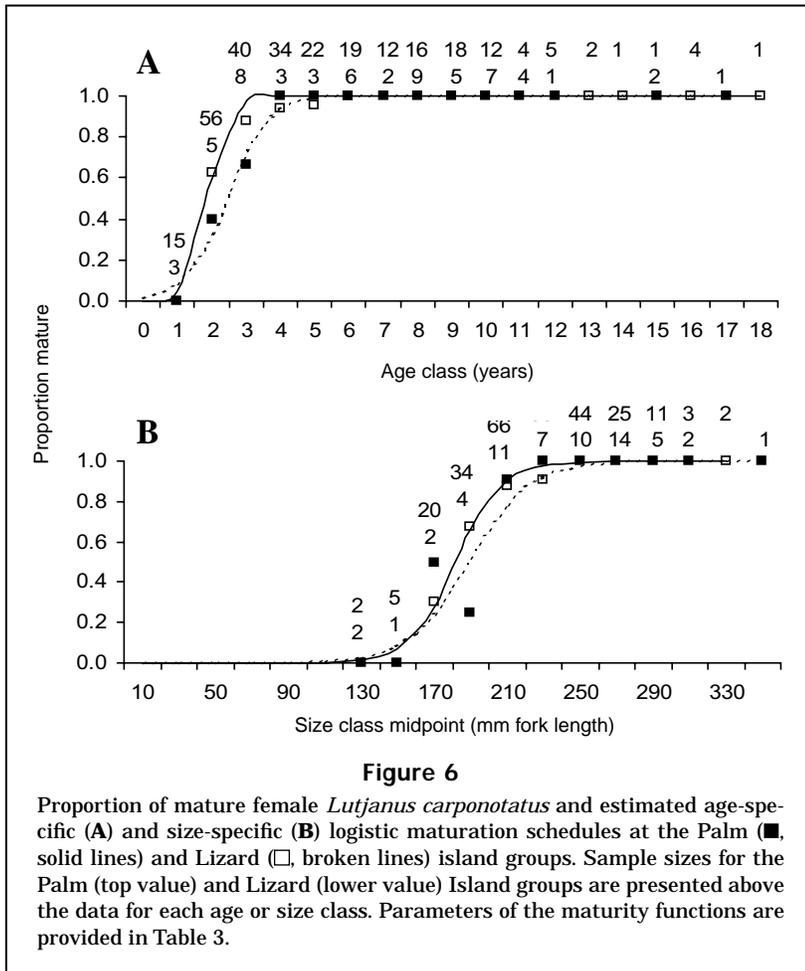
lines across body sizes (Fig. 9A). This suggests that on average GW at stage IV during peak spawning months is a linear function of TW. Lizard Island group fish generally had larger ovaries at a given size than did Palm Island group fish (Fig. 9A), a difference supported by ANCOVA ($df=1, 125; F=34.7; P<0.001$). In fact, regression slopes of 0.25 and 0.52 suggest relative ovary weights at the Lizard Island group were approximately twice as large as those at the Palm Island group. There were no differences in the GW-TW relationship among October, November, and December at the Palm Island group, and therefore the differences in this relationship between the island groups was

consistent whether only the Palm Island group October data were used or whether the October through December data were used.

Although GW is a linear function of TW, the nonzero regression constants (Fig. 9A) mean that GW is not a constant proportion of TW. Consequently, GSI increases with increasing TW (Fig. 9B). The relationship between TW and GSI is not strong, with regression slopes close to zero and low r^2 values at both island groups (Fig. 9B). Despite this, the relationship is statistically strong at both the Palm (ANOVA: $df=1, 82; F=12.70; P=0.006$) and Lizard (ANOVA: $df= 1, 42; F=22.95; P<0.0001$) Island groups. Also, there is

some suggestion that, like the GW-TW relationship, the GSI-TW relationship varies between the island groups, although to a much lesser extent (ANCOVA: $df=1,125$; $F=7.44$; $P=0.007$).

There is some indication that larger fish spawn over a longer period at the Palm Island group. During the September–February spawning season, mean GSI values were always higher for mature Palm Island group females >230 mm FL compared with mature females ≤ 230 mm FL at the same location (Fig. 10). This pattern is likely due in part to the higher relative gonad weights of larger fish (Fig. 9B) but also seems to be driven by greater proportions of stage-IV ovaries among larger mature females in September, October, and February compared with fish ≤ 230 mm FL (Fig. 10). During these months, 13%, 13% and 25% more large fish were at stage IV, respectively, than were small fish.



Discussion

Demography and reproduction of *L. carponotatus*

Growth of *L. carponotatus* is rapid for the first two years of life, slows over the next two years, and nearly ceases by age 4. The slowing and cessation of growth coincide with the ages at 50% and 100% maturity, respectively, and support the argument of Day and Taylor (1997) that maturation represents a pivotal physiological transformation and consequently a fundamental shift in the growth trajectory. Further supporting the idea that reproductive development occurs at the expense of somatic growth is the apparently longer average spawning season among larger fish that have ceased most somatic growth. The limited growth over much of the lifes-

Table 3

Parameters of age- and size-specific logistic maturation schedules and estimated ages and fork lengths at 50% maturity of female *Lutjanus carponotatus* at the Palm and Lizard Island groups, Great Barrier Reef. a adjusts the position of the logistic function along the abscissa; r determines the steepness of the logistic function; t_{50} is the age at 50% maturity; L_{50} is the fork length at 50% maturity. Standard errors are provided below parameter estimates.

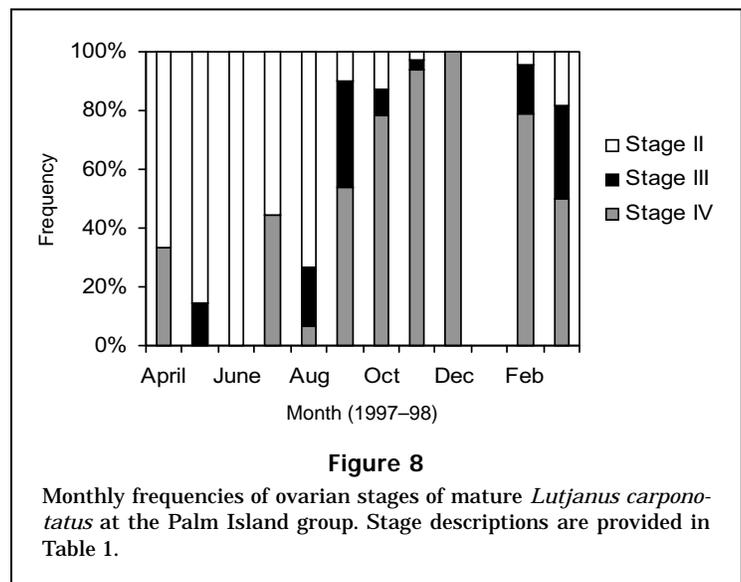
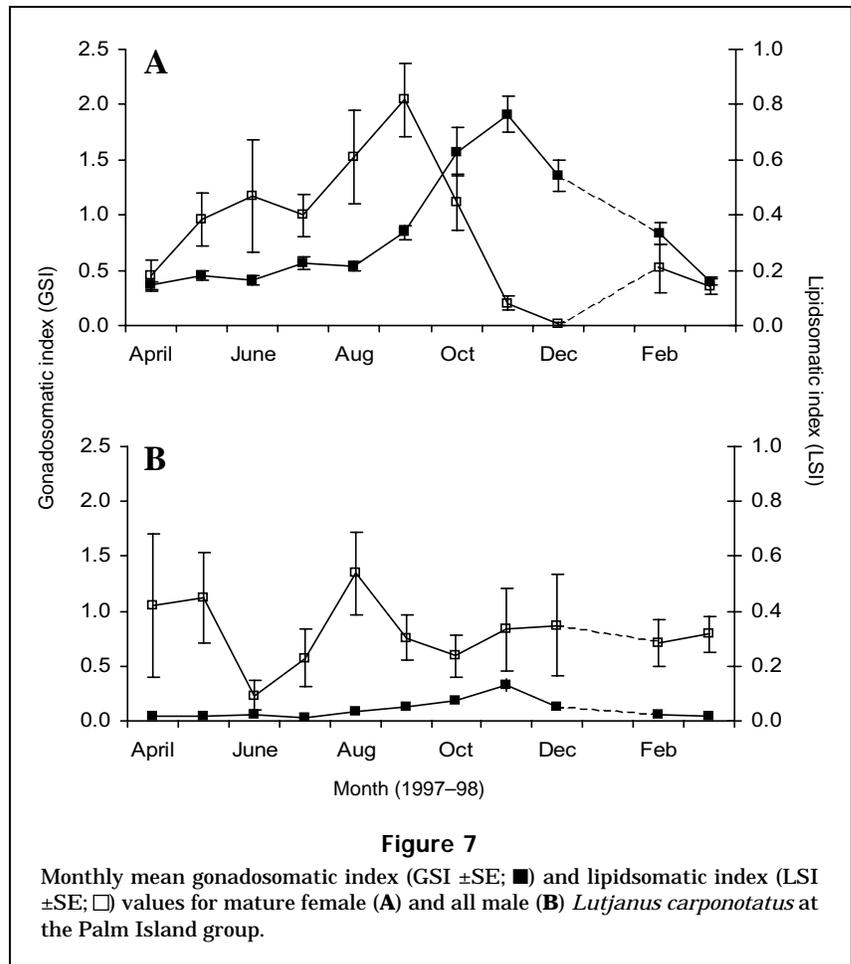
	a	r	r^2	t_{50} or L_{50}
Age-specific				
Palm Island group	6.40 (1.42)	3.42 (0.12)	0.985	1.9 years
Lizard Island group	4.16 (0.48)	1.73 (0.19)	0.990	2.4 years
Size-specific				
Palm Island group	14.72 (1.49)	0.081 (0.008)	0.994	182 mm
Lizard Island group	11.61 (3.84)	0.061 (0.020)	0.908	189 mm

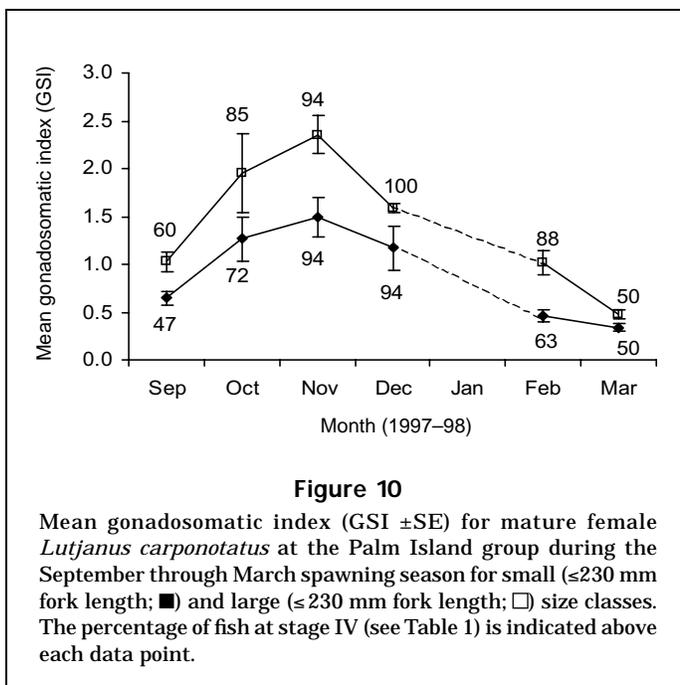
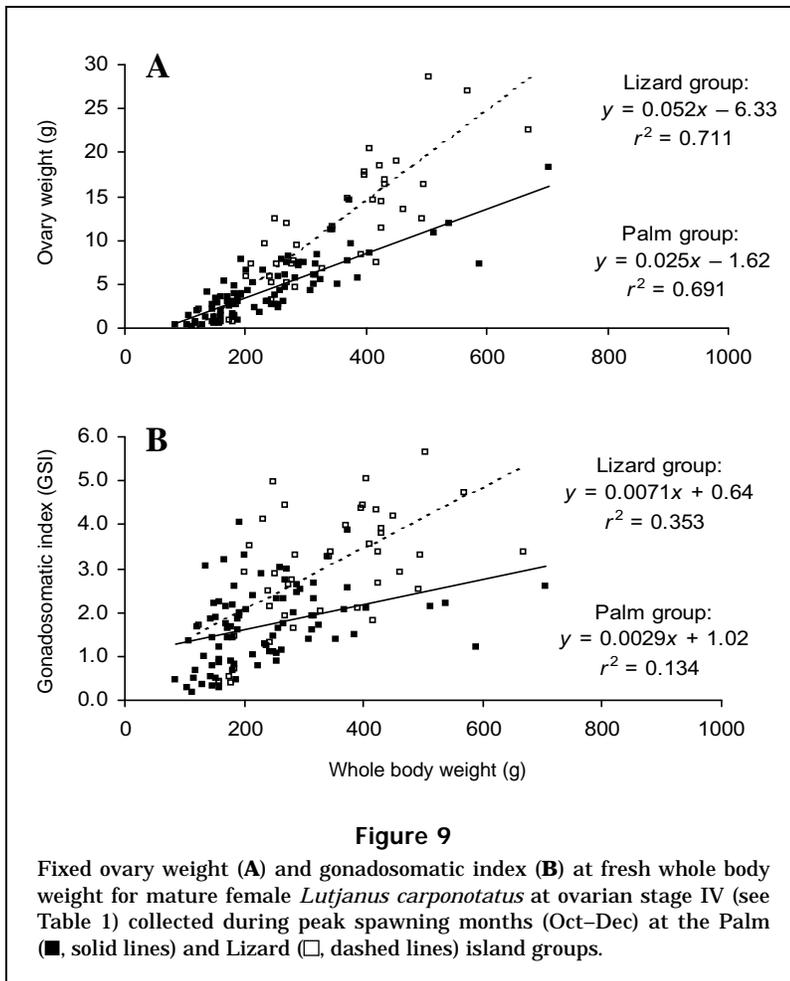
pan of *L. carponotatus* can explain the apparently constant mortality rate over many age classes (evidenced by high catch curve r^2 values) given that mortality is often largely a function of body size (Roff, 1992).

The development and regression of visceral fat stores preceding increases in ovary weight is a pattern that has been observed in other reef fishes, including tropical surgeonfishes (Acanthuridae: Fishelson et al., 1985) and groupers (Serranidae: Ferreira, 1995) and temperate rockfishes (Scorpaenidae: Guillemot et al., 1985). These patterns suggest that the stored lipid is fuelling the energetic costs of spawning. The lack of a similar pattern for males supports the idea that energetic costs associated with production of sperm are low in relation to eggs (Wootton, 1985) thus enabling male *L. carponotatus* to attain larger sizes, as also reported by Newman et al. (2000). Alternatively, males might spawn more frequently throughout the year than females and the lack of seasonal patterns in lipid storage among males might reflect a more regular energetic demand that precludes energy storage. In any case, these sex-specific growth patterns, coupled with similar mortality rates between the sexes and sex ratios that are at unity or that are at most only slightly female-biased (see below), suggest that females are limiting reproduction of this species. Therefore stock dynamics should be modeled in terms of female biology (Hilborn and Walters, 1992).

The apparently female-biased sex ratio at the Palm Island group starkly contrasts with the heavily male-biased sex ratio reported for mid-shelf reefs of the central GBR by Newman et al. (2000). However, neither a male- nor female-biased sex ratio would be expected from a nonhermaphrodite that is not known to possess a complex mating system such as defense of females or territories. It is possible that the spawning sex ratio (i.e. excluding juveniles) is closer to unity if males mature earlier than females, but this ratio is not possible to assess because male maturation has not yet been examined for this species. The difference between the sex ratio reported in this study and that by Newman et al. (2000) might be due to variation in mating systems across a cross-shelf density gradient (Newman and Williams, 1996). Alternatively, the sampling by traps and line fishing conducted by Newman et al. (2000) could be more heavily biased toward males than the sampling by spear fishing used in the present study because of larger

size, wider gape, or more aggressive behavior toward bait among males (Cappo and Brown, 1996). Furthermore, it is likely that a female-biased sex ratio as observed at the





Palm Island group is not a prevalent feature of *L. carponotatus* populations. Rather, the strong statistical suggestion of a sex ratio quite different from unity might be due to the fact that sex ratios often show temporal variability (e.g. Stergiou et al., 1996) coupled with the propensity to achieve statistically significant differences when using large sample sizes (Johnson, 1999).

Maturation schedules and sex-specific growth differences were consistent between the island groups, but overall growth patterns differed, with Lizard Island group fish reaching larger asymptotic body sizes. Given the vast distance between the island groups, these differences might be due to inherent genetic differences between the populations. Or, effects of temperature (the Palm Island group sits at a higher latitude), turbidity, freshwater run-off (the Palm Island group sits closer to a river mouth and has more developed mangrove systems), or other environmental factors could be driving the differences. Of course, these possibilities are not mutually exclusive.

The larger ovaries observed among Lizard Island females might be due to further spatial differences or might be an effect of timing of sampling. The temporal resolution of sampling aimed to identify the extent of the spawning season but was too coarse to account for intramonth differences in ovarian development. Large changes in ovary size might occur within stage IV, and the final progression to immediate prespawning stages can be rapid (e.g. Davis and West,

1993). The Lizard Island group sample was collected from 17 to 23 October 1998, whereas the corresponding Palm Island group sample was collected from 11 to 12 October 1998. The October 1998 new moon was on the 20th, and *P. leopardus*, the only GBR species for which lunar spawning patterns have been reported, spawns primarily around the new moon (Samoilys, 1997). If *L. carponotatus* spawning is also centered around the new moon, the spatial differences in ovary weight at body weight might be due to more advanced development toward full hydration within the Lizard Island group sample. In fact, the higher proportion of stage-IV ovaries within the October Lizard Island group sample (96%) compared with the October Palm Island group sample (78%), coupled with the higher relative ovary weights at the Lizard Island group in October, can be taken as preliminary evidence that *L. carponotatus* spawns at the new moon.

Comparison with other reef fishes

The growth differences between male and female *L. carponotatus* contrast with a general trend of larger body sizes among female lutjanids observed in Atlan-

tic, Caribbean, and Hawaiian species (Grimes, 1987). However, the pattern observed in the present study seems common in the Indo-Pacific where males frequently (Davis and West, 1992; McPherson and Squire, 1992; Newman et al., 1996, 2000), but not universally (Hilomen, 1997), are the larger sex. As noted above, these differences are consistent with predictions based on energetic costs of producing sperm and eggs.

Lutjanus carponotatus spawning patterns identified by using both GSI and ovarian stage frequencies show pronounced seasonal differences: there are at least five months of very limited or no spawning activity from April through August. This finding supports Grimes's (1987) observation that continental lutjanid populations tend to have more restricted spawning seasons than populations associated with oceanic islands, which spawn more or less continuously throughout the year. Although seasonal patterns exist, the prominence of ripe gonads over seven months from September through March suggests an extended spawning season and supports the general observation that tropical reef fishes spawn over longer periods within the year than do cooler water species (Lowe-McConnell, 1979). However, a study with finer temporal resolution is needed to verify that spawning actually occurs in months with a high proportion of stage-IV ovaries.

Female *L. carponotatus* mature on average at approximately 75% of their mean asymptotic size, 54% of their maximum observed size, and 11% of their maximum longevity. The relative size at maturity contrasts with Grimes's (1987) observations that shallow-water continental lutjanid populations like those of *L. carponotatus* on the GBR typically mature at smaller relative sizes ($\approx 42\%$ maximum size) compared to deep-water populations associated with oceanic islands ($\approx 50\%$ maximum size). Two sympatric shallow-water species, *L. russelli* (Sheaves, 1995) and *L. fulviflamma* (Hilomen, 1997), likewise contrast with the general familial trend and mature at approximately 50% and 75% of their maximum size, respectively. Hence, a general pattern of relative size at maturity might exist among shallow-water lutjanids in the GBR region that is different from those regions covered by Grimes's (1987) review. Lutjanids on the GBR are generally lightly fished (Mapstone et al.¹); therefore the geographic difference in sizes at maturity might be due to fishing pressure selecting for smaller sizes at maturity in other regions.

The relative age at maturity of *L. carponotatus* cannot be as readily placed in a broader familial context given that ages at maturity were not widely estimated for lutjanids at the time of Grimes's (1987) review. However, an array of published studies suggests that many tropical and subtropical demersal fishes share the absolute, but not relative, ages of *L. carponotatus* at 50% and 100% maturity at 2 and 4 years, respectively. These include other small gonochores on the GBR (Sheaves, 1995; Hart and Russ, 1996; Hilomen, 1997), as well as a range of gonochores in other regions (Grimes and Huntsman, 1980; Davis and West, 1993; Ross et al., 1995) and hermaphrodites on the GBR and elsewhere (Ferreira, 1993, 1995; Bullock and Murphy, 1994). The ubiquity of this maturity schedule, despite a wide array of maximum body sizes (160–1200 mm) and longevitys (6–56

years) among these species, perhaps suggests a common physiological threshold toward which many species gravitate in order to maximize lifetime reproductive success. More comprehensive analysis of life history trade-offs (e.g. Roff, 1992) is needed to test this hypothesis.

Fisheries management

Harvest of *L. carponotatus* is currently restricted to fish greater than 250 mm total length (approximately 233 mm FL) with the aim of allowing 50% of fish to spawn at least once, and this regulation is proposed to remain after revision by the GBR fishery management plan (Queensland Fisheries Management Authority³). The estimated size at 50% maturity of 190 mm FL suggests that the regulation is meeting its objective. However, the objective itself might not adequately protect the reproductive potential of *L. carponotatus* and similar species if individuals require multiple spawning years to ensure sufficient replenishment of the stock. The extensive longevitys of many reef fishes have been hypothesized to be a mechanism for coping with low and irregular recruitment rates through a process dubbed the "storage effect" (Warner and Chesson, 1985). The rationale behind the storage effect hypothesis is that fish must reproduce during many breeding seasons in order to endure poor recruitment years and realize high reproductive success during the unpredictable and intermittent good recruitment years. If this process is important for population dynamics of *L. carponotatus* and other species, management will need to protect an intact natural population structure in some areas within the fishery. Protecting older age classes cannot be achieved by using maximum size limits for species like *L. carponotatus* that have a pronounced asymptote in the growth trajectory because body sizes are similar over a broad range of age classes and size is therefore poorly correlated with age. Protecting natural age structure could be accomplished through a system of strategically designed marine protected areas that allow some populations to experience natural survival free of fishing mortality.

Proposed closures of the GBR line fishery during nine-day periods around the new moon in October, November, and December are aimed at protecting spawning activity and particularly spawning aggregations of *P. leopardus* and other harvested species (Queensland Fisheries Management Authority³). *Lutjanus carponotatus* shares a peak spawning period during these months with *P. leopardus* (Ferreira, 1995; Samoily 1997) and several other sympatric exploited species (McPherson et al., 1992; Sheaves, 1995; Hilomen, 1997; Brown et al.⁵). In addition, the larger ovaries of the Lizard Island group fish, which were collected closer to the new moon, may indicate that, like *P. leopardus* (Samoily 1997), *L. carponotatus* spawns at

⁵ Brown, I. W., P. J. Doherty, B. Ferreira, C. Keenan, G. McPherson, G. Russ, M. Samoily, and W. Sumpton. 1994. Growth, reproduction and recruitment of Great Barrier Reef food fish stocks. Final report to the Fisheries Research and Development Corporation, FRDC Project 90/18, Queensland Department of Primary Industries, 154 p. Southern Fisheries Centre, GPO Box 76, Deception Bay, Queensland 4508, Australia.

the new moon. Therefore, the timing of the proposed spawning closures seems appropriate. However, it is not known whether *L. carponotatus* aggregate to spawn; therefore the goal of protecting spawning aggregations might not be relevant for this species. In fact, the prevalence and ecological importance of spawning aggregations for any species on the GBR is largely unknown; therefore the efficacy of the proposed closures is difficult to predict.

Beyond the implications for management regulations, these data have implications for modeling *L. carponotatus* stock dynamics. In particular, the results suggest that reproductive output by a unit of *L. carponotatus* biomass cannot be predicted on the basis of that biomass alone. Relative ovary weight increases slightly with increasing body size and there is evidence that larger fish spawn more frequently. The greatest difference in the proportion of ripe ovaries between size classes occurred in February 1998 after severe flooding in January. It is possible that the lower proportion of ripe ovaries among small fish in February was due to stresses caused by changes in salinity or increased run-off and is not a regular trait. However, increased resilience to environmental stresses that allows more frequent spawning would also increase the relative reproductive success of large fish. Therefore, a population comprising fewer larger fish is likely to show greater annual egg production than a population with equivalent biomass that comprises more numerous but smaller fish. Additionally, the sex-specific patterns reported in this study further suggest gross biomass might be an inadequate index of replenishment potential and that female biomass needs to be considered. Therefore, stock structure, in terms of sex ratio and the frequency of size classes, and not simply overall biomass needs to be considered when predicting reproductive potential.

Acknowledgments

I thank the numerous assistants who participated in fieldwork, as well as Sam Adams and Sue Reilly for assistance with histological examinations. The manuscript was greatly improved by comments from Howard Choat, Carl Walters, Tony Fowler, Campbell Davies, Sam Adams, Bruce Mapstone, an anonymous thesis examiner, and two anonymous reviewers. This work was conducted while the author was supported by an international postgraduate research scholarship from the Commonwealth of Australia and a postgraduate stipend from the CRC Reef Research Centre. Final preparation of the manuscript took place while the author was supported by a postdoctoral fellowship funded jointly by the University of Windsor and the Canadian National Science and Engineering Research Council (collaborative research opportunity grant no. 227965-00) to Peter Sale and others).

Literature cited

- Adams, S., B. D. Mapstone, G. R. Russ, and C. R. Davies.
2000. Geographic variation in the sex ratio, sex specific size,

- and age structure of *Plectropomus leopardus* (Serranidae) between reefs open and closed to fishing on the Great Barrier Reef. *Can. J. Fish. Aquatic Sci.* 57: 1448–1458.
- Bullock, L. H., and M. D. Murphy.
1994. Aspects of the life history of the yellowmouth grouper, *Mycteroperca interstitialis*, in the eastern Gulf of Mexico. *Bull. Mar. Sci.* 55:30–45.
- Cappo, M., and I. W. Brown.
1996. Evaluation of sampling methods for reef fish of commercial and recreational interest. CRC Reef Research Centre Technical Report 6, 72 p.
- Cappo, M., P. Eden, S. J. Newman, and S. Robertson.
2000. A new approach to validation of periodicity and timing of opaque zone formation in the otoliths of eleven species of *Lutjanus* from the central Great Barrier Reef. *Fish. Bull.* 98:474–488.
- Connell, S. D.
1998. Patterns of piscivory by resident predatory reef fish at One Tree Reef, Great Barrier Reef. *Mar. Freshw. Res.* 49:25–30.
- Dalzell, P.
1996. Catch rates, selectivity and yields of reef fishing. *In* Reef fisheries (N. V. C. Polunin and C. M. Roberts, eds.), p. 161–192. Chapman and Hall, London.
- Davies, C. R.
1995. Patterns of movement of three species of coral reef fish on the Great Barrier Reef. Ph.D. diss, 212 p. James Cook University, Queensland, Australia.
- Davis, T. L. O., and G. J. West.
1992. Growth and mortality of *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia. *Fish. Bull.* 90:395–404.
1993. Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia. *Fish. Bull.* 91: 224–236.
- Day, T., and P. D. Taylor.
1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. *Am. Nat.* 149: 381–393.
- Everhart, W. H., and W. D. Youngs.
1981. Principles of fishery science, 349 p. Cornell Univ. Press, Ithaca, NY.
- Ferreira, B. P.
1993. Reproduction of the inshore coral trout *Plectropomus maculatus* (Perciformes: Serranidae) from the central Great Barrier Reef, Australia. *J. Fish Biol.* 42:831–844.
1995. Reproduction of the common coral trout *Plectropomus leopardus* (Serranidae: Epinephelinae) from the central and northern Great Barrier Reef, Australia. *Bull. Mar. Sci.* 56: 653–669.
- Ferreira, B. P., and G. R. Russ
1994. Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus*, (Lacepede 1802) from Lizard Island, northern Great Barrier Reef. *Fish. Bull.* 92:46–57.
- Fishelson, L., W. L. Montgomery, and A. A. Myrberg.
1985. A new fat body associated with the gonad of surgeonfishes (Acanthuridae: Teleostei). *Mar. Biol.* 86:109–112.
- Grimes, C. B.
1987. Reproductive biology of the Lutjanidae: a review. *In* Tropical snappers and groupers: biology and fisheries management (J. Polovina and S. Ralston., eds.), p. 239–294. Westview Press, London.
- Grimes, C. B., and G. R. Huntsman.
1980. Reproductive biology of the vermilion snapper,

- Rhomboplites aurorubens*, from North Carolina and South Carolina. *Fish. Bull.* 78:137–146.
- Guillemot, P. J., R. J. Larson, and W. H. Lenarz.
1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae: *Sebastes*). *Fish. Bull.* 83:299–311.
- Ha, P. Y., and R. A. Kinzie.
1996. Reproductive biology of *Awaous guamensis*, an amphidromous Hawaiian goby. *Environ. Biol. Fish.* 45:383–396.
- Hart, A. M. and G. R. Russ.
1996. Response of herbivorous fishes to crown-of-thorns *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus*. *Mar. Ecol. Prog. Ser.* 136:25–35.
- Higgs, J. B.
1993. A descriptive analysis of records of the recreational reef-line fishery on the Great Barrier Reef. M.Sc. thesis, 128 p. James Cook Univ., Queensland, Australia.
- Hilborn, R., and C. J. Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty, 570 p. Kluwer Academic, Boston, MA.
- Hilomen, V. V.
1997. Inter- and intra-habitat movement patterns and population dynamics of small reef fishes of commercial and recreational significance. Ph.D. diss., 277 p. James Cook Univ., Queensland, Australia.
- Hoenig, J. M.
1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* 82:898–902.
- Johnson, D. H.
1999. The insignificance of statistical significance testing. *J. Wildlife Manag.* 63:763–772.
- Kimura, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull.* 77:765–776.
- Kritzer, J. P.
2002. Variation in the population biology of stripey bass *Lutjanus carponotatus* within and between two island groups on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 243:191–207.
2003. Biology and management of small snappers on the Great Barrier Reef. In *Bridging the gap: a workshop linking student research with fisheries stakeholders* (A. J. Williams, D. J. Welch, G. Muldoon, R. Marriott, J. P. Kritzer, and S. Adams eds.), p. 62–80. CRC Reef Research Centre, Townsville, Queensland, Australia.
- Kritzer, J. P., C. R. Davies, and B. D. Mapstone
2001. Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates. *Can. J. Fish. Aquat. Sci.* 58: 1557–1568.
- Lobel, P. S.
1989. Ocean current variability and the spawning season of Hawaiian reef fishes. *Env. Biol. Fish.* 24:161–171.
- Lowe-McConnell, R. H.
1979. Ecological aspects of seasonality in fishes of tropical waters. *Symp. Zool. Soc. Lond.* 44:219–241.
- McPherson, G. R., and L. Squire
1992. Age and growth of three dominant *Lutjanus* species of the Great Barrier Reef inter-reef fishery. *Asian Fish. Sci.* 5:25–36.
- McPherson, G.R., L. Squire, and J. O'Brien
1992. Reproduction of three dominant *Lutjanus* species of the Great Barrier Reef inter-reef fishery. *Asian Fish. Sci.* 5:15–24.
- Murphy, M. D.
1997. Bias in Chapman-Robson and least-squares estimators of mortality rates for steady state populations. *Fish. Bull.* 95:863–868.
- Newman, S. J., and D. M. Williams
1996. Variation in reef associated assemblages of the Lutjanidae and Lethrinidae at different distances offshore in the central Great Barrier Reef. *Environ. Biol. Fish.* 46: 123–138.
- Newman, S. J., D. M. Williams, and G. R. Russ
1996. Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the central Great Barrier Reef, Australia. *Mar. Freshw. Res.* 47:575–584.
1997. Patterns of zonation of assemblages of the Lutjanidae, Lethrinidae and Serranidae (Epinephelinae) within and among mid-shelf and outer-shelf reefs in the central Great Barrier Reef. *Mar. Freshw. Res.* 48:119–128.
- Newman, S. J., M. Cappel, and D. M. Williams
2000. Age, growth and mortality of the stripey, *Lutjanus carponotatus* (Richardson) and the brown-stripe snapper, *L. vitta* (Quoy and Gaimard) from the central Great Barrier Reef, Australia. *Fish. Res.* 48:263–275.
- Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations, 382 p. *Bull. Fish. Res. Board Can.* 191.
- Roff, D.A.
1992. The evolution of life histories, 535 p. Chapman and Hall, New York, NY.
- Ross, J. L., T. M. Stevens, and D. S. Vaughan
1995. Age, growth, mortality, and reproductive biology of red drums in North Carolina waters. *Trans. Am. Fish. Soc.* 124:37–54.
- Samoilys, M. A.
1997. Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) on the northern Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 160: 149–159.
- Samoilys, M. A., and A. Roelofs.
2000. Defining the reproductive biology of a large serranid, *Plectropomus leopardus*. CRC Reef Research Centre Technical Report 31, 36 p.
- Sheaves, M.
1995. Large lutjanid and serranid fishes in tropical estuaries: are they adults or juveniles? *Mar. Ecol. Prog. Ser.* 129: 31–40.
- Stergiou, K. I., P. Economidis, and A. Sinis.
1996. Sex ratio, spawning season and size at maturity of red bandfish in the western Aegean Sea. *J. Fish. Biol.* 49: 561–572.
- Warner, R. R., and P. L. Chesson.
1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* 125:769–787.
- West, G.
1990. Methods of assessing ovarian development in fishes: a review. *Aust. J. Mar. Freshw. Res.* 41:199–222.
- Wootton, R. J.
1985. Energetics of reproduction. In *Fish energetics: new perspectives* (P. Tytler and P. Calow, eds.), p. 231–254. Croom Helm, London.